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canadensis into mounds created for tree
seedling establishment
Final Report 1997




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September 1997

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SIMON. M. LANDHÄUSSER AND VICTOR J. LIEFFERS

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Disclaimer

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Abstract

Rhizome recruitment of *Calamagrostis canadensis* into mounds created for tree seedling establishment

by

SIMON. M. LANDHÄUSSER AND VICTOR J. LIEFFERS

In a series of four experiments we investigated rhizome spread and growth of *C. canadensis* into mounds. Three experiments were established in the field. The first field experiment tested the effectiveness of mineral soil caps thickness of mounds and the importance of clonal connections to plants outside the mounds. The two other field experiments investigated the effect of organic layer removal prior mounding and the effect of increased moisture and nutrient levels on the rhizome penetration and distribution from *C. canadensis* plants outside of the mound. Mound thickness was the most important factor determining the success of *C. canadensis* establishment. Clonal connections were only of importance at the thin mineral soil cap, where larger amounts of rhizome biomass grew through the mounds supported by rhizome connections from the outside of the mound. Removing the organic horizons prior to mound construction resulted in a reduction of *C. canadensis* establishment on mounds. After two growing seasons, the spread of rhizomes from plants outside of the mound into the mineral soil cap was not strongly affected by the fertiliser and moisture treatments. The fourth experiment was conducted under a controlled environment, testing the ability of rhizomes from buried *C. canadensis* sods, which had been pre-treated with two levels of light and nutrients, to grow through mineral soil caps of different thickness. Treating *C. canadensis* with low light and nutrients reduced carbohydrate concentrations in rhizomes by 20% and rhizome biomass by 42%. Despite low carbohydrate reserves, the sprouting ability of rhizomes through the mineral soil cap was equal to the control. Strategies of *C. canadensis* establishment on mound are discussed. Thicker mounds

and mounds where the organic horizons containing most of the rhizomes were removed prior to mound formation had the lowest establishment of the grass. The series of experiments support the use of mounding as a silvicultural tool for tree establishment on sites with grass competition problems.

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Table of contents

DISCLAIMER.....	ii
ABSTRACT.....	iii
ACKNOWLEDGEMENTS	v
TABLE OF CONTENTS.....	vi
LIST OF FIGURES.....	vii
INTRODUCTION	1
MATERIALS AND METHODS	3
EXPERIMENT 1.....	3
EXPERIMENT 2.....	3
EXPERIMENT 3.....	4
EXPERIMENT 4.....	5
RESULTS.....	8
EXPERIMENT 1.....	8
EXPERIMENT 2.....	8
EXPERIMENT 3.....	9
EXPERIMENT 4.....	11
DISCUSSION	15
LITERATURE CITED	18

List of Figures

FIGURE 1: (a.) Maximum height and above-ground dry weight of C. canadensis in response to the sand and/or fertilising treatment. (b.) Dry weight of rhizomes growing (1) into the mineral soil cap, (2) growing outside of the mound, (3) growing in the organic layer beneath the mound, and (4) their combined dry weight in response to the four treatment combinations.

FIGURE 2: Total non-structural carbohydrate (TNC) concentration in non-emerged rhizomes of C. canadensis plants which had been subjected to high and low light and nutrients regimes. TNC was measured prior to the burial of the sods and at the end of the experiment (2 months later).

FIGURE 3: The number of emerging tillers and rhizomes and their biomass in response to three mineral soil caps (5, 15, 25 cm) of C. canadensis sods which had been buried for 2 months. Calamagrostis canadensis sods had been pre-treated prior to the experiment with two levels of nutrients and light, resulting in different carbohydrate reserves.

FIGURE 4: The relationships of total non-structural carbohydrate (TNC) concentration in non-emerged rhizomes with the number of tillers and their above-ground biomass.

Introduction

Calamagrostis canadensis (Michx.) Beauv. (bluejoint or marsh reed grass) is a highly competitive grass which dominates rich, moist forest sites following clearcutting. It poses a serious problem for Picea glauca (Moench.) Voss (white spruce) reforestation (Drew 1988; Lieffers et al. 1993). Calamagrostis canadensis has the ability to colonise and rapidly dominate disturbed areas by clonal spread of rhizomes (Ahlgren 1960; Dyrness and Norum 1983). Ground scarification methods are used for temporary exclusion of major competitor species through the removal of their roots and rhizomes in order to enhance both the natural and artificial regeneration of P. glauca (Tappeiner 1979, Hungerford 1985, McMinn and Hedin 1990). Mounding as a silvicultural site preparation method is widely used in Fennoscandia (Örlander et al. 1990) and has become an alternative to other site preparations like blading or plowing in northern boreal forest sites where high water tables and/or heavy competition are a problem. Apart from excluding major competitors, mounds provide the tree seedling with higher soil temperatures, better aeration, and well drained conditions, due to the elevated planting location (Örlander et al. 1990).

Excavators or specialised mounding equipment are used to create this elevated position over an inverted soil profile (a layer of organic matter topped by a mineral soil cap). Under some circumstances mounds effectively prevent the grass from colonising that location for three or more years (long enough to establish P. glauca seedlings) (Bedford and McMinn 1990). However, in other situations, the grass will grow through the mound and colonise much of the surface area in a relative short time period. The mechanisms for rhizome colonisation into the mounds is not clear. There are two possible sources for C. canadensis rhizomes to spread into the mound; firstly, by rhizomes already present in or under the mound and/or secondly, from plants outside of the mound, pushing rhizomes into the mound.

The rhizome mass of C. canadensis is mostly confined to the organic layer or the organic/mineral soil interface and rhizomes of C. canadensis are rarely found in the mineral soil layer (Younkin 1974; Lieffers et al. 1993). If the beds of C. canadensis are well established on a site, the rhizomes will have large reserves of stored carbohydrates that will be available for the growth through and the colonisation of the

mound (Hogg and Lieffers 1991_a, _b). Extensive clonal connections might also allow portions of the clone outside of the mound to supply resources for growth of the rhizomes inside the mound. Both these factors may allow for rapid colonisation of a newly created mound. Thick mineral soil caps may act as an impediment for rhizome growth through the mound from the deeply buried rhizomes (Landhäusser et al. 1996). Assuming a classic inverted mound is created, the rhizomes entering the mound from the outside should grow largely horizontally following the organic layers at the bottom of the mound; however, it is not clear whether the rhizome will move along temperature, moisture or nutrient gradients which has been observed in rhizomes of other species (Cook 1983, Salzman 1985).

The objectives of this study were (1) to test the effectiveness of various thickness' of the mineral soil caps and the importance of clonal connections to plants outside the mounds on sites with well established C. canadensis clones; (2) to investigate the effect of removal of the organic layer prior to inverting the mound (screef) on the colonisation of C. canadensis on mounds; (3) to determine the effects of increased moisture and nutrient levels of the mineral cap on the penetration and distribution of rhizomes from plants outside of the mound; and (4) to test in a controlled environment the ability of rhizomes from buried C. canadensis sods with different amounts of carbohydrate reserves to grow through mineral soil of different thickness.

Materials and Methods

Experiment 1

The objective was to test the effectiveness of various thicknesses of mineral soil cap of mounds and the importance of clonal connections to parts of the clone outside of the mound. The experimental area was located across a 30 ha clearcut about 30 km north-east of Dixonville, Alberta (56° 42' N, 117° 50' E). The site was a P. glauca dominated mixed wood site before it was cut in 1994. In the fall of 1994, a total of 56 mounds were created using an excavator backhoe. The mounds were located in areas with some established swards of C. canadensis which had the potential to become dominated by the grass. Half of the mounds had a mineral cap of 23 cm (layer of the B or C horizons, silty clay), the other half had a mineral cap of 10 cm. The duff layer (LFH horizons) for all mounds was 10 cm. The diameter of all mounds was approximately 80 cm. On half of the mounds for each mineral cap thickness the rhizome connections to the outside of the mound were severed with vertical cuts with a sharp spade. In the analysis, only mounds were used which had C. canadensis plants next to them and therefore had the potential of being colonised by the grass. The dry weight of C. canadensis shoots emerging through the mounds was determined in late August of 1996 and again in the late summer of 1997. The experiment was a 2x2 factorial design with mineral soil cap thickness and trenching as the main factors. Analysis of variance was used to test for differences in C. canadensis above-ground dry weights among cap thicknesses and clonal connections. The frequency of C. canadensis occurring on the different mounds was tested using categorical data modelling (CATMOD) procedure in SAS (SAS Institute Inc. Cary, NC, Version 6.12).

Experiment 2

The objective was to assess the effect of back-screefing the litter layer prior to mound formation to reduce C. canadensis recolonisation of the mound. On the same clearcut as in experiment 1, a total of 40 mound were created by a backhoe in the fall of 1994; the mineral soil cap for all mounds was on average 23 cm. Mounds were created

also in areas with established swards of C. canadensis. Half of the mounds had the litter layer removed with a scraping action (back-screef) of the backhoe prior inverting the mound on that position. This removed a considerable amount of the organic layer which is thought to contain the majority of rhizomes. Therefore, only a thin layer of LFH horizons was incorporated into the mound. As in the experiment 1, only those mounds, which had C. canadensis plants in the proximity of the mounds, were used in the analysis. In 1996 and 1997, above-ground dry weight of C. canadensis on each mound was determined. The experiment was analysed using one-way analysis of variance with the screef treatment as the main factor and differences in the frequency of C. canadensis occurring on the mounds were tested using categorical data modelling.

Experiment 3

In this experiment the degree of and orientation of rhizome expansion of C. canadensis into mounds of different fertility and moisture content was assessed on sites where the grass was not well established prior mounding. In the fall of 1994, a total of 64 mounds were established on the same clearcut mentioned in experiment 1, but on parts of the clearcut where there were only negligible amounts of C. canadensis prior to mounding. The mineral soil cap of the mounds was on average 25 cm and the diameter was 80 cm. Half the mounds were covered in 1995 and resanded in 1996 with a 3 cm sand layer to inhibit evaporation from the mound surface therefore, increased soil moisture (Örlander et al. 1990). Half of the mounds with and without sand had the mineral soil cap fertilised with (30 g 14-14-14 N-P-K, slow release fertiliser in early June of 1995 and 1996) which was spread over the surface of the mound. The experimental design was a 2x2 factorial design with the sand cover and fertiliser treatment as the two main factors. In late June 1995, three established potted C. canadensis plants (grown from rhizome fragments in a greenhouse in 10 cm diameter pots for three months) were planted on the edge of each of the mounds at the organic matter-mineral soil interface.

The plants were allowed to grow for two growing seasons. During the two summers soil temperatures and moisture content was monitored during different times of the growing season. Soil temperature in the mounds was determined using

copper/constantan thermocouples installed 10 cm into the mineral soil cap and in the organic matter of the mound. Soil moisture was determined at 10 cm depth in the mineral soil cap by extracting a small soil sample for weighing and drying to determine the percent water content. In the fall of 1996, after the two growing seasons, one of the three C. canadensis plants was randomly selected for harvesting. The selected plant was carefully excavated from the mound and rhizomes were assigned to one of the three following categories (1) rhizomes growing into the mineral soil cap (2) rhizomes growing in the organic layer underneath the mound, and (3) rhizomes growing away from the mound. The total dry weight of rhizomes and maximum length in the three categories were measured. Total above-ground dry weight and height of the C. canadensis plants were also measured. After removing the plant, the mound was reformed and the remaining plants allowed to regrow. In 1997, above-ground dry weight of rhizomes which had sprouted through the mound was determined. Response variables were analysed with analysis of variance testing for differences among the fertiliser and sand cover treatments.

Experiment 4

This growth chamber study evaluated the impact of rhizome carbohydrate reserves and mound thickness on the sprouting of C. canadensis through a mineral soil cap. Sods of grass with different levels of carbohydrate reserves were produced as follows: Three germinating seeds of C. canadensis, collected from central Alberta, were planted into 48 shallow bulb pots (25 cm diameter, 15 cm deep) and kept under a clear plastic sheet for 2 weeks and then transferred to a growth chamber. The plants were grown in a peat-vermiculite soil mixture (Metro Mix 290, Terra Lite 2000, W. R. Grace & Co. of Canada Ltd., Ajax, Ontario, Canada) for 14 weeks in either high light ($300 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD), fluorescent bulbs) and high nutrient regimes (200 ml of 2 g L^{-1} N-P₂O₅-K₂O; 20-20-20 with chelated micronutrients weekly for the weeks 3 to 6 and then twice a week for weeks 7 to 10) or secondly in half the light and nutrient regimes. Prior to the next stage of the experiment, the plants were hardened by reducing nutrition and temperatures, and shortening day lengths. For week 11 and 12, the fertiliser regime was reduced to 100

ml (50 ml in low treatment) of $2 \text{ g L}^{-1} \text{ N-P}_2\text{O}_5\text{-K}_2\text{O}$; 20-20-20 weekly, and in week 13 and 14 no fertiliser was applied. The growth chamber conditions during the 14 weeks were: for week 3 to 10, 18 hours light and 6 hours dark cycle with a day temperature of 20°C and night temperature of 18°C ; week 11-12, 15/9 light/dark cycle with $17/12^\circ\text{C}$ day/night temperature; week 13, 12/12 cycle with $8/5^\circ\text{C}$. In week 14, the C. canadensis plants were transferred to a freezer with no light and a temperature of -1°C .

Prior to covering the sods, the dead leaves and shoots of the hardened C. canadensis plants were cut off 5 cm above the soil surface. The above-ground dry weight was determined for all pots and rhizome dry weight was determined in three pots from each carbohydrate reserve treatment. The grass sods were removed from the remaining 42 pots and equal mass of rhizome segments from the edge of each pot were collected for carbohydrate analysis. The sods of grass were then planted into the bottom of large cylindrical plastic pots 43 cm in diameter and 38 cm tall. The planting medium was peat-vermiculite soil mixture which was also used to cover the sods to a depth of 6 cm. The peat-vermiculite mixture was moistened with 200 ml of $1 \text{ g L}^{-1} \text{ N-P}_2\text{O}_5\text{-K}_2\text{O}$; 20-20-20 (same for all treatments). The sods were then covered with a mineral soil, a mixture of B and C horizons of a silty-clay Luvisolic soil collected at an aspen forest in central Alberta. Four mineral soil capping thicknesses were superimposed on the two carbohydrate reserve treatments, no-cap, 5, 15, and 25 cm caps. The no-cap treatment (control) was replicated five times, while the other treatments were replicated 7 times for a total of 52 pots. For each thickness the same volume of mineral soil was used and compacted to the desired height; this ensured a similar compaction for all the replicates (bulk densities of about 0.9 Mg m^{-3}). This is comparable to bulk densities found in mounds in the field after one year of freeze/thaw cycles break the soil into smaller fragments (McNabb 1994).

The pots were placed into a growth chamber, watered periodically to maintain moist conditions, and grown for 2 months. For all pots the growth chamber conditions were 18 hours light and 6 hours dark cycle with a day temperature of 20°C and night temperature of 18°C and light levels at $300 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD. The date of the first emergence of sprouts at the soil surface for each pot was noted. Half the pots with a mineral soil cap of 5 cm had C. canadensis sprouts emerging after 10 days, at a 15 cm

mineral soil cap half the pots had sprouts 25 days since the burial of the sods, and at a mineral soil cap thickness of 25 cm half the pots had sprouts after 46 days. The time of emergence did not differ between the carbohydrate reserve treatments. After 8 weeks (61 days) the experiment was terminated, assuming that at that time sods which had not sprouted above the soil surface were depleted of their carbohydrate reserves and were dead.

Rhizomes and their above-ground material were collected and divided into the following categories: (1) rhizomes originating from the buried mother plan which either had emerged (produced above-ground parts) or not (non-emerged) while growing through more than 90% of the height of the mineral soil cap and (2) rhizomes (emerged or non-emerged) which had grown along the side of the pot (through less than 90% of the mineral soil cap). In each category if applicable, the height of the longest leaf and the number of sprouts, and the dry weight of the above-ground parts was determined. Further, the number of rhizomes, their number of branches, and the dry weight of the rhizomes were measured within each category. Rhizome samples were collected for carbohydrate analysis from non-emerged rhizomes in the pots with 15 and 25 cm mineral soil cap.

For total non-structural carbohydrates (TNC) analysis, rhizomes were dried at 68°C and ground through a 40-mesh screen in a Wiley mill and stored at -12°C prior to analysis. TNC was measured by digesting the samples in 0.005N sulphuric acid and sugar concentrations were determined with a phenolsulphuric acid assay (Smith et al. 1964). TNC was calculated as percent of dry weight. Response variables were tested with analysis of variance procedures and linear regression was used to investigate the relationships among carbohydrate concentrations in rhizomes and the above-ground material grown through the mineral soil cap.

Results

Experiment 1

In 1996, the frequency of C. canadensis growing through the mounds was higher in the mounds with the 10 cm mineral soil cap (12 of the 16 acceptable mounds) than with the 23 cm mineral soil cap (8 of the 23 acceptable mounds) ($p=0.0172$). Overall, trenching had no effect on the frequency of mounds with C. canadensis growing through the mound. In terms of the amount of above-ground dry weight of C. canadensis, however, the biomass on mounds capped with 10 cm was 1.1 g on the trenched mounds compared to 21.4 g on the non-trenched mounds. While on mounds with a mineral soil cap of 23 cm this response was not detectable with 0.74 g and 0.81 g for the trenched and the non-trenched treatment, respectively (mound thickness \times trenching $p=0.0046$).

Similar to 1996, the frequency of mounds occupied by C. canadensis was still higher in 1997 on mounds with a 10 cm mineral soil cap compared to the 23 cm thick mineral soil cap and as in 1996 the trenching treatment had no effect on the frequency of mounds with C. canadensis growing through the mound. Overall the biomass of above-ground material was higher in 1997 than in 1996; however, the differences detected in 1996 were still present. Trenching had an effect on the mounds with a 10 cm mineral soil cap (38.1 g for the non-trenched compared to 16.6 g for the trenched mounds), while on mounds with a mineral soil cap of 23 cm above-ground dry weight did not differ for both trenching treatments (4.8 g) (mound thickness \times trenching $p=0.0045$).

Experiment 2

Back-screefing the organic soil layer prior the mounding resulted in reduced frequencies of C. canadensis occurring on top of the mounds in 1996. Nine of the 16 acceptable back-screefed mounds were occupied by C. canadensis, while without a screef treatment 12 of the 12 acceptable mounds were occupied by C. canadensis

($p=0.002$). Back-screefing, however, had no effect on the height or above-ground dry weight of C. canadensis compared to the unscreefed mounds.

In 1997, however, differences in above-ground dry weight of C. canadensis between the screefed and the non-screefed mounds were evident. Mounds with a back-screef treatment had with an average dry weight of 3.23 g, only 13.3% of the C. canadensis than mounds without the back-screef treatment (24.2 g) ($p=0.0016$). The frequency of mounds occupied by C. canadensis was still higher (12 of 12) in the non-screefed treatment than in the mounds with the back-screef treatment (7 of 16) ($p=0.0003$).

Experiment 3

Covering the mounds with sand did not result in a detectable higher moisture content or soil temperatures at 10 and 27 cm depth compared to the unsanded mounds. This resulted in undetectable differences in all measured response variables between the sand treatments (Fig. 1a, b). Fertilising resulted in increased height ($p=0.0269$) and above-ground dry weight ($p=0.0082$) of the planted grass plants and also in an increase in total dry weight of rhizomes and sprouts originating from these plants ($p=0.0356$) (Fig. 1). Fertilising the mounds increased the total dry weight of rhizomes and their sprouts by 55% from an average of 20.2 g to 31.2 g. When broken down into the three different categories of (1) rhizomes growing into the mineral soil cap (2) rhizomes growing in the organic layer underneath the mound, and (3) rhizomes growing away from the mound, increases in rhizome dry weight due to fertilising was only detectable in rhizomes growing in the organic layer underneath the mound ($p=0.05$) and in rhizomes growing away from the mound ($p=0.074$) (Fig. 1b). Average maximum length of rhizomes growing in the organic layer underneath the mound was higher when fertilised, growing about 53 cm in length under fertilised conditions compared to 42.5 cm in the unfertilised mounds ($p=0.0334$). There was no difference in dry weight ($p=0.4575$) and maximum length ($p=0.893$) between the fertiliser treatments for rhizomes growing into the mineral soil cap (Fig. 1b). Rhizomes in the mineral soil cap was lower (mean of 1.4 g dry weight) compared to rhizomes growing away from the mound (4.9 g) or growing in the organic layer under the mound (7.3 g). There were also no differences in the frequency of C. canadensis

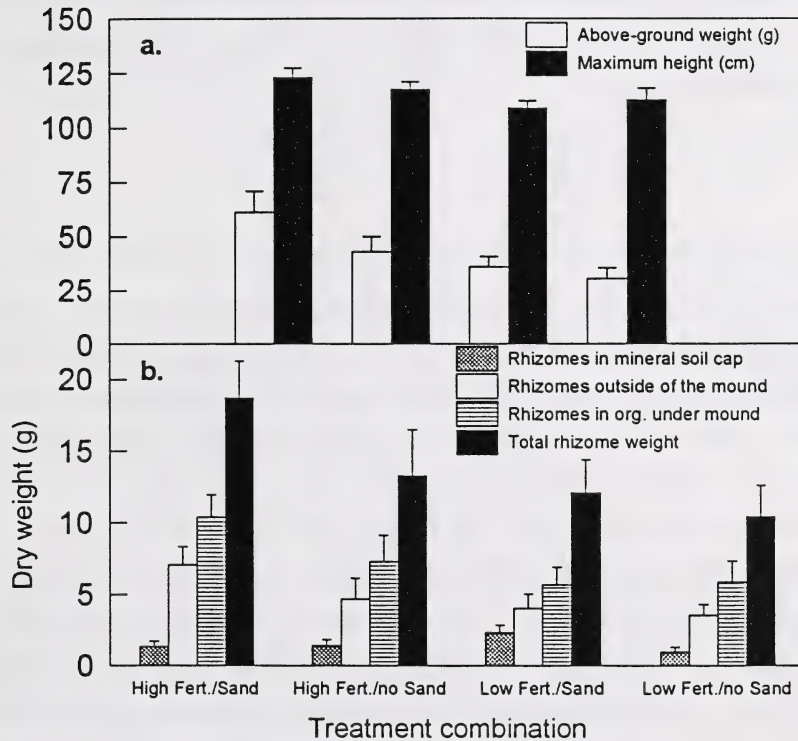


FIGURE 1: (a.) Maximum height and above-ground dry weight of *C. canadensis* in response to the sand and/or fertilising treatment. (b.) Dry weight of rhizomes growing (1) into the mineral soil cap, (2) growing outside of the mound, (3) growing in the organic layer beneath the mound, and (4) their combined dry weight in response to the four treatment combinations.

sprouting through the mineral soil cap of the mounds for both the fertiliser ($p=0.5836$) and the sand treatments ($p=0.9679$).

In 1997, the dry weight of above-ground parts of C. canadensis which had emerged through the mineral soil cap was not different for the treatments and there were also no differences in the frequencies of mounds which were occupied by C. canadensis. An average of 7.7 g of above-ground dry weight of C. canadensis had grown through the mounds.

Experiment 4

Only data from rhizomes which had grown through more than 90% of the mineral soil cap were used in this study. Less than 10% of the total dry weight was from rhizomes which had grown along the edge of the container and not grown through the mound. The pre-treatments with high light and fertiliser resulted in larger C. canadensis plants, with 29.5 g above-ground material for the high pre-treatment compared to 20.4 g for the low pre-treatment ($p=0.0001$). Although the average dry weight of rhizomes for the pre-treatment was 12 g for the high and 7 g for the low pre-treatment, a statistically significant difference due to the pre-treatment was not detectable, this was probably due to the low sample size ($n=3$) ($p=0.146$). The high pre-treatment, however, resulted into higher concentrations of total non-structural carbohydrate (TNC) in rhizomes (17.6% of the dry weight) compared to in the low pre-treatment (14.4%) ($p=0.0011$) (Fig. 2).

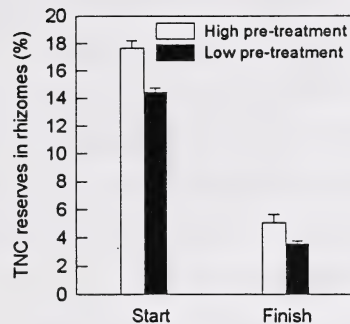


FIGURE 2: Total non-structural carbohydrate (TNC) concentration in non-emerged rhizomes of *C. canadensis* plants which had been subjected to high and low light and nutrients regimes. TNC was measured prior to the experiment and at the end of the experiment (2 months later).

After eight weeks since burial of the sods, most measured variables did not show a significant response to the pre-treatment. A pre-treatment effect (P) was only detectable in the dry weight of the rhizomes, which had grown through the mineral soil cap and produced above-ground shoots (emerged rhizomes) (Fig. 3). The pre-treatment resulted into different magnitudes of response to the different thickness of the mineral soil cap (M). At the high pre-treatment, the dry weight of emerged rhizomes was only reduced when the mineral soil cap was 25 cm thick, while at the low pre-treatment, the biomass of emerged rhizomes decreased already at a mineral soil cap height of 15 cm ($P \times M$ interaction $p=0.0246$) (Fig. 3). At the high pre-treatment, the rhizome dry weight of emerging rhizomes decreased from an average of 3.7 g for both mineral soil caps of 5 and 15 cm to 0.3 g at 25 cm, while at the low pre-treatment the rhizome dry weight decreased from 3.1 g at 5 cm, to 1.4 g at 15 cm, and further to 0.4 g at a 25 cm mineral soil cap. Above-ground dry weight ($p=0.1173$) and number of tillers ($p=0.07$) of the emerged rhizomes was not different for the pre-treatment, but both variables strongly decreased ($p=0.0001$ and $p=0.0001$) with an increase of the mineral

soil cap thickness (Fig. 3). Total non-structural carbohydrate concentration did not affect the number of rhizomes which were able to emerge above the mineral soil cap ($p=0.2523$), but increasing the thickness of the mineral soil cap resulted into a strong reduction of the number of rhizomes growing through the mound ($p=0.0001$) (Fig. 3). On average 23 rhizomes reached the surface at a 5 cm mineral soil cap, 11.5 at 15 cm, and 1.8 rhizomes at 25 cm. When the rhizomes reached the soil surface and produced leaves and tillers, they started to produce on average 2.3 rhizome branches, which was about ten times higher than in those rhizomes which had not yet emerged through the mineral soil cap (0.16 branches per rhizome).

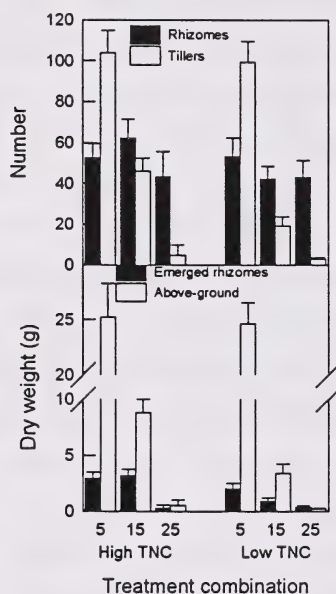


FIGURE 3: The number of emerging tillers and rhizomes and their biomass in response to three mineral soil caps (5, 15, 25 cm) of *C. canadensis* sods which had been buried for 2 months. *Calamagrostis canadensis* sods had been pre-treated prior to the experiment with two levels of nutrients and light, resulting in different carbohydrate reserves.

Covering the *C. canadensis* sods with a mineral soil cap of 15 or 25 cm resulted in a drastic reduction of TNC concentration over the two months period (Fig. 2). Total non-structural carbohydrate reserves in both treatments were reduced by 71% and 75% for the high and low pre-treatment, respectively. Differences in TNC concentrations between both pre-treatments with 5.07% at the high and 3.57% at the low pre-treatment were still detectable two months later ($p=0.0176$) (Fig. 2). Regression analysis showed a positive relationship between the amount of above-ground dry weight of emerged rhizomes (grown through the mineral soil cap) and the concentration of total non-structural carbohydrates (TNC) in rhizomes, which had not emerged through the mineral soil cap (dry weight = $-3.804 + 1.93\% \text{TNC}$; $p=0.0006$; $R^2=0.56$) (Fig. 4). While the above-ground variables were well correlated with the amount of TNC in non-emerged rhizomes, the total number ($p=0.8314$) and dry weight of rhizomes ($p=0.072$) was not strongly correlated with the amount of TNC (Fig. 4).

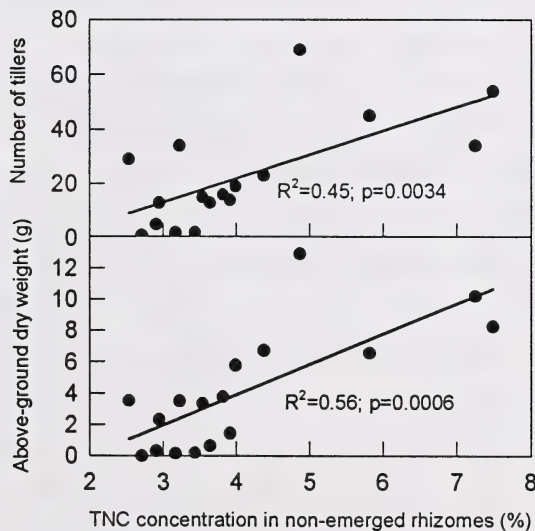


FIGURE 4: The relationships of total non-structural carbohydrate (TNC) concentration in non-emerged rhizomes with the number of tillers and their above-ground biomass.

Discussion

In experiment 1 which tested the importance of the mineral soil cap thickness of mounds and the clonal connections to parts of the clone outside of the mound, the mound thickness was the most important factor determining the success of C. canadensis establishment on the mound via rhizome spread. Clonal connections were only of importance at the thin mineral soil cap, where a large amount of rhizomes had to be supported from the outside of the mound. At a thin mineral soil cap, a large number of rhizomes expanded towards the soil surface. This suggests that a larger number of rhizomes might need initially more support from the plants outside of the mound.

The importance of the LFH horizons as a rhizome bank and as a growing space for C. canadensis rhizomes has been documented in experiment 2. Removing the LFH horizons (back-screef treatment) resulted in a reduction of C. canadensis establishment on the mounds. This treatment, however, removes an important source of nutrients in the mound which is reflected in the poor growth of the grass when it did grow through the mounds. It is also likely to result in slower tree growth on back-screefed mounds.

Experiment 3, which tested the degree and orientation of rhizome expansion of C. canadensis into mounds, showed the strong preference of C. canadensis to expand its rhizomes through the LFH horizons, even when covered by a mound. The fertiliser treatment which was superimposed on the mounds resulted in greater growth of the parent plant, but did not result in a higher rate of C. canadensis establishment on the mound. This suggests that rhizomes do not follow a nutrient gradient, since the source of fertiliser was on the top of the mound which should result into an increase in rhizomes growing towards the nutrient source. Calamagrostis canadensis has been described to display an opportunistic guerrilla strategy for clonal foraging (Lovett Doust 1981) by "choosing" with their long rhizomes more favourable habitats (Macdonald and Lieffers 1993). This suggests a preference of C. canadensis rhizomes to grow through a substrate which provides lower mechanical impedance (organic horizons) than a mineral soils does which has been observed in an earlier study (Landhäusser et al. 1996). The sand treatment, which was suppose to increase soil moisture in the mound, failed, largely due to difficulties to keep the mound top and sides covered with sand.

The importance of mineral soil cap thickness was also apparently in experiment 4, where a mineral soil cap of 25 cm resulted in a large reduction of sprouts from rhizomes. At this mineral soil cap thickness, it took on average of 46 days until half the pots had sprouts on the soil surface. Carbohydrate concentration at the end of the experiment in rhizomes which had not reached the surface were on average 4.3% of the dry weight from 16% before the burial of the sods. The pre-treatments in experiment 4 showed, however, the importance of light and nutrients for the accumulation of non-structural carbohydrates reserves in rhizomes. A reduction of light and nutrients by 50% resulted in a reduction of the carbohydrate concentration in the rhizomes by about 20%, a reduction of the above-ground biomass by about 33%, and a reduction of the rhizome biomass by about 42%. Translocation of carbohydrates from above-ground parts of the clone which had sprouted through the mineral soil cap did likely occur. Carbohydrates were translocated from the above-ground parts through the connection with the buried mother plant providing other rhizomes with carbohydrates. This is supported by the correlation of carbohydrate concentration in non-emerged rhizomes with the number of tillers or their above-ground biomass (Fig. 4).

The reasons for rhizomes not growing in the mineral cap and mostly being confined to the organic layer are not quite clear. Increased bulk density (soil strength) might play a major role in the rhizome distribution in the mound. Landhäusser et al. (1996) showed that high bulk density showed a strong reduction of rhizome expansion into mineral soils, even if there is a supply of nutrients available. The few rhizomes which grew into and through the mineral soil cap have the potential of producing ramets which could supply the older parts of the clone with carbohydrates as seen in experiment 4. Once established on the mound the ramets can become independent and start expanding laterally into the mound with new rhizomes originating from the base of the ramet. This has been observed in experiment 4, where the rhizomes, once they had grown through the mineral soil cap, produced lateral rhizomes, facilitating the lateral spread over the mound surface. The importance of rhizome connection is also corroborated by the results in experiment 1 where trenching resulted in a reduction of C. canadensis sprouts occupying the mound.

The strategy of a deeply buried C. canadensis sod (>15 cm mineral soil cap) as seen in experiment 4, was to expand first a few rhizomes towards the soil surface. It can be speculated that apical dominance, which has been observed in C. canadensis (Powelson and Lieffers 1991), suppressed the branching of rhizomes from axillary buds and the expansion of a large number of rhizomes from the buried sod. This resulted in an allocation of more energy towards only a few expanding rhizomes. Once these few rhizomes reached the soil surface, the apical dominance of the apex broke down and other rhizomes of the clone, supported through translocation, expanded and grew towards the soil surface. At a thin mineral soil cap this strategy was not detectable. Apical dominance in the growing apex of rhizomes in other grass species has been observed in several studies and has been linked to hormonal activities (Rogan and Smith 1976) and/or nutrient status (Qureshi and McIntyre 1979).

The results of these experiments support the use of mounding as a silvicultural tool in the development of safe sites for tree establishment in grass dominated sites. The experiments showed that mounds with mineral soil caps greater than 23 cm provide considerably better suppression of C. canadensis than thinner caps. The studies further showed that removal of some or all of the organic matter, which contains the majority of C. canadensis rhizomes, prior to mounding will further reduce the possibility of C. canadensis colonisation on the mound. This removal of the organic matter, however, could also have some negative effects for the planted tree seedling (e.g. nutrient and moisture supply). If an organic layer in the mound is preferred, the study showed that the majority of rhizomes stayed within the organic layer and only a few rhizomes will grow into the mineral soil cap after two years. However, once C. canadensis grows through the mounds we speculate, it will occupy more and more of the mound over the next years. If the soil strength in the mound is high the lateral expansion of the grass will be slow (Landhäusser et al. 1996). By the time C. canadensis fully occupies the mound, the planted trees should be large enough to withstand the shade and mechanical damage associated with the grass.

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